

# ON THE NERVOUS SYSTEM OF THE LARVA OF CORYDALIS CORNUTA L.\*

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Owing to its large size and to the ease with which the parts may be dissected, the larva of *Corydalis cornuta* L. is especially favorable for the study of the nervous system. In spite of this fact, only fragmentary work has been done upon this species, and the present investigation was undertaken for the purpose of making a comprehensive study of the larval nervous system as well as for verifying the work already done.

Leidy '48 pictures and describes in a general way the nervous system of the adult insect, which in various respects differs from that of the larva. The only general discussion of the larval nervous system is that of Comstock and Kellogg '95. Though thoroughly accurate, this description is very concise, covering only the features of interest to the elementary student.

A detailed study of a limited region is that of Krauss '87, who confined his studies to the nervous system of the head of the larva. Although inaccurate in some details, his work is a valuable contribution to the knowledge of the nervous system and has been of much value to me in preparing this paper.

In 1895 an investigation was begun by Miss M. A. Nichols, for the purpose of determining the existence of a secondary nervous system such as that described by Newport '32 and '34. Unfortunately, this work was never finished, though promising interesting results. The notes and drawings were deposited in the entomological library of Cornell University, and in the study of certain features have been used to advantage by the writer.

For the material used, I am indebted to my friend, Mr. C. W. Palmer, of Westtown, Pa., who on different occasions has been kind enough to send me an abundant supply of living larvae from that locality. To Prof. J. H. Comstock I wish here to express my sincere acknowledgment for aid and encouragement liberally bestowed. For suggestions and aid received from members of the Entomological Staff of Cornell University, and most especially from Prof. W. A. Riley, under whose guidance this investigation has been carried on—I wish to express my sincere gratitude.

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\* Contribution from the Entomological Laboratory of Cornell University.

## METHODS.

The usual methods of dissection were employed in making the preliminary studies of the nervous system. On account of the transparency of the tissues, however, it was found necessary to supplement the examination of fresh specimens with the study of stained or fixed specimens in which the nerves were more clearly differentiated. For such preparations alcoholic picric acid solution has been used to very great advantage. It stains and hardens the tissues rapidly, so that the preparation can be used almost without delay. The specimens when immersed for a longer time (2 - 3 hours) in water will destain, but they can be restained any number of times desired.

Alcoholic sublimate (Gilson's fluid) is very effective in differentiating the tissues. It must, however, be borne in mind that sublimate is very corrosive to metals, and a black precipitate is quickly formed, when metal pins or tools are used.

In tracing certain nerves *intra vitam* staining with methylene blue has been used to advantage, but since the different nerves take up the stain very irregularly\*, much time and patience has been required to secure satisfactory results. The living larva was injected with approximately 1-2 cc. of the solution ( $\frac{1}{2}$ % methylene blue in normal salt solution). Half an hour later it was etherized and opened along the back and then spread out on a sheet of cork, exposing the visceral cavity. The still living tissues were kept moist with the above solution until the desired results were obtained. It sometimes requires 3-5 hours before certain nerves take up the stain. Once stained they will retain it for only a short time. By the application of a few drops of hydrogen peroxide solution ( $H_2O_2$ ) the stain is intensified.

It was found that for some features a process of maceration could be used to great advantage. By soaking for several days in water considerable amount of muscular tissue is loosened and can be washed off easily by moving the preparation in water, leaving the more resistant nerves exposed and distinct. Similar results were brought about by the use of 5-10% nitric acid solution. In either of these two processes, the preparation must be afterwards hardened in alcoholic picric acid. These methods should first be used after a general study of the nervous system has been made.

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\* According to Ehrlich '86 (Biol. Centralb., VI, p. 214) the sensory nerves are the first stained, while the motor nerves require longer time.

## INTRODUCTION.

The *Corydalis* larva, popularly known under the name of "dobson," "hellgrammite" or "crawler," is commonly found under stones at the bottom of swiftly flowing streams. Three years are required to complete the life cycle of the insect. The pupal and adult stages are of short duration, so that almost three years are required for the development of the larva.

This, when full grown, measures from 80 to 90 millimeters in length. It is rather oblong, depressed and tapering towards the posterior extremity. The entire body is dark brown or nearly black in color, with irregular markings on the chitinized portions of the head and thorax.

On either side of the head, caudad of the base of the antennae, there are six simple eyes. In very rare instances are there developed seven perfect eyes, the rudiments of the seventh being indicated by a light spot below the normal ones.

There are nine distinct abdominal segments, the last of which is provided with a pair of prolegs. The lateral borders of the first eight abdominal segments are pushed out into so-called lateral filaments. There is also a small pair of similar filaments to be found on the prolegs. On the ventral side of each of the first seven abdominal segments, there is a pair of large tracheal gills of a brush-like appearance. These are well supplied with tracheae, which ramify rapidly and send off branches, one to each separate thread-like portion of the gill.

As might be expected from the systematic position of the *Corydalis*, the nervous system of the larva is of a very generalized type. There is a ganglion for practically each segment of the body. Only in the last abdominal segments has there taken place a cephalization by the fusion of two or possibly three ganglia. The various ganglia of the central nervous system are connected longitudinally by two distinct nerve cords or connectives\*, thus forming a chain, which extends on the ventral side throughout the length of the body. In the thorax and in the first abdominal segment, the ganglia are situated near the floor below the large ventral muscles, while the succeeding abdominal ganglia are all found above the same muscles.

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\* In accordance with the suggestion of E. Yung '78, I have maintained the term *connectives* for the longitudinal nerve cords, while the term *commissure* has been used only for the transverse connections of symmetrical parts of the ganglia.

In the following consideration of the details of the larval nervous system I shall first take up the discussion of the central system, and follow this by a consideration of the so-called sympathetic system.

### THE CENTRAL NERVOUS SYSTEM.

THE SUPRAOESOPHAGEAL GANGLIA OR BRAIN (Figs. 4 and 7, *b, b*). The so-called brain consists of two, large ovoid ganglia, situated dorsad of the oesophagus in the anterior portion of the head and immediately beneath the roof of the head, being protected only by a thin layer of connective tissue. The two ganglia are connected by a short, thick commissure, which in the drawing (Fig. 4) is indicated by the constriction between the two halves.

The dorsal portion of the anterior enlarged end of the aorta (Fig. 4, 7, *ao*) is attached to the caudo-ventral border of the brain.

In the brain of the *Corydalis* larva, the neuromeres—protocerebrum, deutocerebrum, tritocerebrum—are not so well differentiated as in the brain of Orthopterous insects studied by Viallanes '87, yet indications of the primitive ganglia constituting the brain are found in the form of basal enlargements of the optic, antennal, and the labral nerves which arise from the corresponding proto-, deuto-, and tritocerebrum. In the brain of the adult *Corydalis*, however, the neuromeres are more prominent than in the larva, the brain having undergone great modification during the pupal stage.

THE OPTIC NERVES (Fig. 4 and 7, *o, o*). The lateral borders of the brain are pushed out into the optic nerve trunks. A short distance from their origin, each trunk divides into seven slender nerves, each of which supplies an ocellus. As already stated, the seventh ocellus is generally rudimentary. The seventh nerve corresponding to this eye, however, is always present.

THE ANTENNAL NERVE (Figs. 4, 5, and 7, *a, a*.) This arises from the side of the brain ventro-cephalad of the optic nerve-trunk. The antennal nerve breaks up into three branches, of which the anterior main branch innervates the antenna. The second branch innervates the muscles of the antenna, situated at the base of the same. The basal branch, a rather slender nerve, originates near the ganglia and extends dorso-laterad.

THE CLYPEO-LABRAL NERVE (Figs. 4, and 7, *cl*). This together with the arched nerve (*ar*), originates as a single nerve trunk

from the base of the crus cerebri or more generally dorsad of the base of the crus cerebri. Under no circumstances could this nerve be considered as originating from the crus, since it is a well established fact that the nerve fibres of the labral nerve arise from the tritocerebrum.

At a distance of from one-half to one millimeter from its point of origin, the clypeo-labral nerve becomes separated from the arched nerve and projects cephalad into the clypeus and labrum, where it breaks up into six branches. The distribution of these is obvious from an examination of figure 4 and need not be discussed in detail. The relation of branch 3 to the sympathetic system is worthy of note.

In addition to the above described nerves of the supra-oesophageal ganglia there is to be found a pair of minute nerves which arise near the middle line of the caudal portion of the brain (Fig. 4.) These project dorso-caudad to the roof of the head.

THE CRURA CEREBRI (Figs. 2, 5, 7, *cr*). The crura cerebri consists of two large nerve cords connecting the supra- and sub-oesophageal ganglia and with them forming the so-called oesophageal ring. Each crus originates from the ventro-lateral border of the brain, turns ventrad around the oesophagus and enters the dorso-lateral border of the suboesophageal ganglion.

THE SUBOESOPHAGEAL COMMISSURE \*(Figs. 2 and 7, *s.c*). Connecting the lower portions of the crura cerebri, and forming a semicircle round the ventral part of the oesophagus is the so-called suboesophageal commissure. This commissure, usually overlooked, has been found in a number of widely separated insects (for summary see Kolbe '93, pp. 411-413). In the most frequently cited instances this commissure originates from the brain, although a position similar to that of the *Corydalis* is reported for *Libellula*, *Dytiscus*, *Carabus*, *Phryganea* and various other insects.

From the suboesophageal commissure there are two cephalad projecting nerves, which innervate the upper longitudinal labial muscles (Fig. 2, *lm*).

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\* Various names have been applied to this commissure. Thus, Lienard '80 calls it: *Les connexions transversales des commissures oesophagiennes*; Kolbe '93 *Quercommissure* or *Schlundring*; Edward Burgess '80: *Cross-nerve* or *commissure between the two hemispheres*; while Packard '98 refers to it as *transverse commissure of the oesophageal ring*. Since these terms are applicable only in limited groups it is preferable to use the term *suboesophageal commissure*.

THE SUBOESOPHAGEAL GANGLION (Figs. 2, 5, and 7, *s.g.*). The suboesophageal ganglion is situated below the oesophagus in the anterior portion of the head. It is a rather large ovoid ganglion with its caudal portion terminating in the two connectives which pass back to the first thoracic ganglion.

From the suboesophageal ganglion there arise the following nerves:

THE MANDIBULAR NERVE (Figs. 4, 5, 6, and 7, *md.*). The mandibular nerve arises as a large nerve trunk from the upper part of cephalo-lateral border of the suboesophageal ganglion. For a distance of a few millimeters it runs cephalad underneath the pharynx, then it turns dorso-laterad until reaching the level of the optic and antennal nerves. Here it projects laterad, passing in front of the column-like apodeme (*ap*), where it divides into three branches.

Branch 1 bends caudad and innervates the large mandibular muscles. Branch 2 is quite short and slender, and connects the mandibular nerve with a minute ganglion (*g*). This ganglion has been observed in several specimens and probably forms a part of the sympathetic system. The third branch of the mandibular nerve has two prominent ramifications, of which the first, labeled 5, enters the mandible while the second, marked 3, runs laterad until approaching the outer condyle of the mandible, where it divides, sending off one anterior smaller branch to this part of the head and one larger caudal branch to the mandibular muscles.

Nerve 4 has not been found connected with the central nervous system. It and the ganglion (*g*) will be discussed under the sympathetic system.

THE MAXILLARY NERVE (Figs. 4, 5, and 7, *mx.*). The maxillary nerve arises from the cephalo-lateral border of the suboesophageal ganglion. It is a rather large nerve trunk, projecting cephalad for the distance of a few millimeters, after which it breaks up into four branches (Fig. 5 *mx.*) The most proximal of these branches consists of a small nerve extending laterad to the base of the maxilla. The three remaining branches all originate from the same level shortly cephalad of the first branch. The two branches of the fourth, and also the anterior branch of the third, enter the maxilla. The second branch terminates in the enlarged basal portion of this organ.

THE LABIAL NERVE (Figs. 5 and 7, *l*). The labial nerve arises slightly ventrad of the maxillary nerve. It runs forward into the labium, where it gives off several branches. The first of these has three sub-branches, of which the proximal one projects mesad and innervates the ventral muscles of the labium; the second terminates in numerous branches near the lateral base of the labium; and the third projects to the latero-distal portions of the submentum.

Branch 2\* arises cephalad of branch 1, and runs mesad of the main nerve. Its termination has not been located definitely. Branch 3 innervates the lateral portions between the submentum and the mentum. Branch 4 supplies the distal border of the labium and branch 5 enters the labial palpus.

THE GUSTATORY NERVES (Fig. 5, *gn*). Projecting cephalad from the anterior border of the suboesophageal ganglion are two thread-like nerves which have been called by Krauss '84 the *gustatory nerves*. They innervate the regions surrounding the opening of the salivary glands.

THE SALIVARY NERVES (Figs. 2, and 5, *sn*). The salivary nerves consist of two long thread-like nerves, arising shortly cephalad of the connectives from the caudo-lateral border of the ganglion. They project caudad, parallel to the connectives and enter the prothoracic cavity, where they turn laterad, branching off near the sides of the prothorax.

It is interesting to note that up to the present time the salivary glands of *Corydalis* have not been described. It was first through the tracing of the nerves and the determining of their homologies that I was led to recognize the salivary duct, the so-called "*unknown nerves*" of Krauss '84.

THE VENTRAL NERVE of the suboesophageal ganglion (Fig. 5, *v*). Slightly caudad of the maxillary nerves there arise from either side of the ganglion a small much branched nerve, which innervates the regions below this ganglion. There is also a short branch given off to the salivary ducts.

THE MEDIAN NERVE (Fig. 5, *m. n*). The median nerve arising from the suboesophageal ganglion will be described under the sympathetic system.

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\* Krauss, '84, figures this branch as innervating the salivary duct. (Fig. II, 7).

## THE GANGLIA AND CONNECTIVES OF THE THORAX.

In the thorax (Figs. 1 and 2) there are three quite similar ganglia, which are the nerve-centers of the pro-, meso- and meta-thoracic segments respectively. These ganglia are situated near the floor, ventrad of the longitudinal-ventral muscles and caudad of the center of each respective segment. They are of relatively large size, circular in outline and decidedly depressed.

The first thoracic ganglion (*I*) is connected with the suboesophageal ganglion by two comparatively long connectives. On entering the prothorax they diverge as illustrated in Fig. 2.

The connectives of the two following segments are but half the length of those described above. They are also distinct from each other, enclosing between them the furcae (*f*) to which the ventral diagonal muscles of corresponding segments are attached.

THE NERVES OF THE FIRST THORACIC GANGLION (Fig. 1, 2, *I*). From either of the lateral borders of this ganglion there arise three nerve-trunks (*A*, *B*, *C*), the first and third of which are as large in diameter as the connectives. The anterior nerve trunk (*A*) extends laterad and breaks up into numerous branches which in Fig. 2 have been labeled: *a*, 1, 2, 3; *b*, 1, 2, 3, and *c*, 1, 2, 3, 4. The origin and direction of these nerves is evident from the illustrations and need not be described in detail. The second branch of *a* passes along the floor of the segment and innervates the neck. Branch 3 also follows the floor of the segment and extends to the caudal portion of the head. Nerve *b* supplies the latero-dorsal portions of the segment; branch 4 of nerve *c* runs cephalo-laterad, innervating the lateral portion of the neck.

Nerve *B* is relatively smaller than either *A* or *C*. It forks near its origin, giving the appearance of two distinct nerves. It innervates the ventral and lateral muscles.

Nerve *C*. The nerve of the leg consists of one large main trunk, which near its origin gives rise to a slender branch.

THE NERVES OF THE SECOND AND THIRD THORACIC GANGLIA (Fig. 2, *II*, *III*). The general distribution of the nerves of the above two ganglia is very much the same and therefore will be described together.

Nerve *A*, which in the larva is a rather small nerve, becomes in the adult quite enlarged and constitutes the *alar nerve*.

Nerve *B* resembles that of ganglion *I* except that it has an additional branch (*1*), which is analogous in appearance and distribution to "*a*" of nerve trunk *A* of the prothoracic ganglion.



Nerve *C*, as described under ganglion *I*, consists of two branches.

THE NERVES OF THE CONNECTIVES (Fig. 2,  $n_1c$ ,  $n_2c$ ,  $n_3c$ ,  $n_4c$ ). From the connectives of the thorax there arise four pairs of nerves of which the first two belong to the prothorax, the third to the mesothorax and the fourth to the metathorax. In their origin from the connectives, these nerves display quite a variation. The first pair may arise from the connectives either in the head or in the prothorax. The two nerves of a pair are not always directly opposite but may arise at different levels.

The nerves of the first pair arising from the connectives ( $n_1c$ ) extend laterad for a short distance receiving branches from the transverse nerve of the sympathetic system. They then turn caudad between the large ventral muscles and terminate in the caudal regions of the prothorax.

The second pair ( $n_2c$ ) arise from the connectives near the first thoracic ganglion. They extend laterad to the sides of the prothoracic segment.

The third ( $n_3c$ ) pair of nerves originates slightly caudad of the middle from the connectives between ganglia *I* and *II*. They extend laterad, one on either side, and give rise to three branches, at the same level, 2-3 millimeters from the base of the main nerve. The first of these branches projects cephalad into the caudal regions of the prothorax; the second extends laterad passing under the large trachea and gives off at this point a slender branch which joins the tracheal nerve. As Fig. 2 shows, this tracheal nerve is connected with the transverse nerve of the sympathetic system; the third branch runs caudo-laterad and passes over the large trachea to the sides of the mesothoracic segment.

The fourth nerve ( $n_4c$ ) originating between the meso- and the metathoracic ganglia, resembles the third and its branches have an analogous distribution and relation to the remainder of the nervous system.

#### THE ABDOMINAL GANGLIA\* AND CONNECTIVES.

The abdominal ganglia consist of eight small ovoid nerve centers, situated below the alimentary canal and above the large ventral muscles. As a rule each ganglion is situated in the

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\* The modification of the first and eighth abdominal ganglia will be described separately.

anterior region of its segment. From above, the ganglia and the proximal portions of their nerves are protected by the ventral diaphragm, the outline of which is indicated in Figs. 1, *d, d*, by dotted lines.

The connectives of the abdominal ganglia consist of two distinct cords connecting the successive ganglia. Those of the first and last ganglia are very short because of the cephalization in these regions. The cephalic ends of the connectives are generally closely approximated, while the middle and caudal portions are slightly spread apart, so that the minute median nerve of the sympathetic system becomes exposed between the two connectives. In the abdomen there are no nerves arising from the connectives, such as were found in the thorax.

#### THE NERVES OF THE ABDOMINAL GANGLIA.

The nerves arising from the first seven ganglia are pretty nearly uniform both in number and distribution. Fig. 3, representing the right side of the third segment, illustrates the typical condition of the nerves of the abdominal region. From each ganglion two sets of nerves arise, one pair lateral and one pair ventral.

THE LATERAL NERVE (*l*) extends laterad over the ventral muscles. It gives rise to five branches, which generally extend caudo-laterad to the different parts of the corresponding segment. Branch 1 originates from the cephalic side, near the base of the main trunk. It is a very small nerve and can be detected only in well prepared specimens. The distal end of this branch unites with the transverse nerve (*tr. n.*) forming a single nerve, which extends laterad to the minute *tracheal* nerve\* (*tr. n.*) Branch 2 consists of a large nerve originating from the caudal side, a few millimeters from the base of the main trunk. It extends caudo-laterad over the neighboring muscles (Fig. 1, *m*<sub>1</sub>) and then turns ventrad and innervates the deep lying ventral muscles. Branch 3 arises shortly distad of branch 2. It is a rather large nerve, passing latero-caudad over the ventral muscles. On reaching the outer border of these muscles, the nerve passes underneath a few muscle-fibers (Fig. 1, *m*<sub>2</sub> and Fig. 8, *v*<sub>1</sub> *m*<sub>1</sub>) of the same

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\* Since the nerves of the *tracheal* system have not been considered in this paper, it may be necessary to state that such nerves have been observed lying closely connected with the trachea and in certain instances dividing in such a way as to supply each tracheal branch. The tracheal nerves are connected with both the central and the sympathetic systems.

group. Thus the nerve on passing to the upper portions of the body is protected and held away from the viscera. Branch 4, like branch 3, passes underneath the muscle-fibers of  $m_2$ , then below the larger lateral tracheal tube and innervates the lateral filament. Branch 5 consists of a small nerve which originates from the proximal part of branch 4. It generally extends laterad, passing under the lateral muscle fibers of  $m_2$  (Fig. 1) and extends to the lateral trachea, where it unites with the tracheal nerve described in connection with branch 1.

In the seventh segment, branch 1 of the lateral nerve trunk may be absent. When present, it does not join the transverse nerve as is generally the case in the other segments, but terminates in the ventral diaphragm.

THE VENTRAL NERVE TRUNK ( $v$ ), originates from the ventral side of the ganglion and extends caudo-ventrad innervating various of the more ventral muscles. Branch 4 passes between the muscles and the body-wall and innervates the tracheal gills (Fig. 3, *op.*)

Because of its inconspicuous position this nerve has been very generally overlooked though it is probably to be found in other groups.

THE FIRST ABDOMINAL GANGLION. Unlike the rest of the abdominal ganglia the first is situated below the ventral muscles. It may be located readily by the presence of the diagonal and transverse muscles, which pass dorsad of it (Fig. 1). The nerves of this ganglion are homologous to those of the following ganglia, although they show greater tendency to variation than the latter. Thus branches 1 and 2 may sometimes arise as a single nerve independent of the main lateral nerve. Moreover, branch 1 ramifies more freely than do its homologues of the following segments and it has not been observed to be connected with the transverse nerve, but seems to innervate certain ventral muscles.

THE EIGHTH OR TERMINAL GANGLION (Figs. 10, *G. 8.*) The terminal ganglion of the central nervous system has been pushed cephalad into the central portion or even to the anterior border of the seventh segment, taking the normal position of the seventh ganglion, which, also, has been forced cephalad, and is situated at the caudal border of the sixth segment. The seventh and eighth ganglia are united by two very short connectives, which are generally not longer than the diameter of the last ganglion.

From the large size of the terminal ganglion and because of the numerous nerves arising therefrom, it is evident that it is produced by the fusion of two or more ganglia. Oudemans '87 determined in *Machilis maritima* Latr. that the last abdominal ganglion originated by the fusion of the last three ganglia. On its dorsal side there remained parts of two transverse nerves, which indicated the boundaries of the original ganglia. Such rudiments of the transverse nerves have not been found in the terminal ganglion of the *Corydalis* larva. Influenced, however, by the fact that there are four pairs of nerves arising from this ganglion, we may conclude that these correspond to two lateral and two ventral pairs of nerves of two abdominal ganglia. Although it may be possible to homologize some of these nerves with those of previous ganglia, it cannot be considered conclusive that the last ganglion is produced by the fusion of but two ganglia, since it may be possible that the nerves corresponding to a third have disappeared. An investigation of the embryological condition would be the only way to settle this problem.

Notwithstanding the cephalic displacement of the eighth ganglion, all of its nerves innervate the eighth and terminal segments. As stated above, there are four pairs of nerves arising from this ganglion (Fig. 10 *a, b, c, d*). The first of these originates from the lateral border of the ganglion and runs caudo-laterad to various parts of the eighth segment. The branches of this nerve can readily be homologized with the lateral nerve of previous ganglia. Branch 1, as in some of the previous ganglia, is in this case absent altogether. Branch 2 passes over the large ventral muscle bundle  $m_3$  in the eighth segment and innervates the ventral muscles. Branch 3 supplies the dorsal parts of the segment; branch 4 enters the lateral filament; branch 5 joins the tracheal nerve.

Nerve *b* is homologous with nerve *v* of the previous segment. It originates from the mid-ventral portion of the ganglion and extends caudad, passing underneath the ventral muscles ( $m_3$ ), then turning laterad, innervating approximately the same regions as the ventral nerve of previous ganglia.

Very probably nerves *c* and *d* are homologous to the lateral (*l*) and ventral (*v*) nerve trunks of ganglion 7. Nerve *c* has three prominent branches, the first of which forks giving off one nerve to the lateral filament and one to the proleg. Branch 2 enters the proleg. Branch 3 innervates the reproductive organs as

shown in Fig. 10, passing through the lateral borders of the seminal vesicle.

THE INTESTINAL NERVE\* (Figs. 9 and 10, *in. n*). The intestinal nerves consist of a pair of long, thread-like nerves, which arise from the proximal ends of nerve *c* of the terminal ganglion. They extend cephalad to the second abdominal segment, where they are attached to the sides of the small intestine, shortly caudal of the origin of the Malpighian tubes.

Each proximal portion of these nerves gives rise to five caudad-projecting branches, four of which innervate the hind intestine. The first branch arises from the very base of the intestinal nerve and lies dorsad of nerve *c*. It divides into three sub-branches before reaching the hind intestine. Branches 2, 3, and 4 do not ramify until reaching the intestine. Branch 5 is comparatively small and, unlike the four previous ones, does not reach the intestine, but is attached to a mass of adipose tissue (*ad*).

The intestinal nerves represent the first or basal branch of the lateral nerve, but in distribution they differ radically from that of this branch in preceding segments. It is probable that the suppression of the respiratory nerve, originally occurring between the ganglia represented, and the in-pushing of the proctodaeum are sufficient to account for these modifications, great as they appear.

### THE SYMPATHETIC NERVOUS SYSTEM.

The sympathetic system is divided into the UPPER SYMPATHETIC SYSTEM, lying above the alimentary canal, and the LOWER SYMPATHETIC SYSTEM, lying below it.

The nerves and ganglia of this system are very minute and constitute a supplementary system intimately connected with the central system. Most of the nerves are susceptible to methylene-blue and can best be studied in specimens prepared with this stain.

*The* UPPER SYMPATHETIC SYSTEM is confined to the anterior dorsal portion of the alimentary canal and most particularly to the pharynx and oesophagus within the head. It can be divided into an UNPAIRED MEDIAN and a PAIRED LATERAL SYSTEM.

THE UNPAIRED MEDIAN, STOMOGASTRIC, or, as it is more generally termed, the VAGUS SYSTEM, consists of the following parts:

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\* Comstock & Kellogg, '04, p. 49.

THE ARCHED NERVE (Fig. 4 and 7, *ar*). The arched nerves connect the vagus system with the central system. They arise in connection with the clypeo-labral nerves, one from each upper basal portion of the crus cerebri, and bend mesad so as to meet in the frontal ganglion.

THE FRONTAL GANGLION (*fg*). This ganglion consists of a very minute nerve center, situated a short distance in front of the supraoesophageal ganglia, with which it is connected by an exceedingly fine nerve strand. (Fig. 7, *i*).

THE FRONTAL NERVE (Figs. 4, 7, *f*). The frontal nerve arises from the anterior border of the frontal ganglion and extends cephalad into the clypeus, where it bifurcates.

THE PHARYNGEAL NERVE (Figs. 4, 7, *pn*). From either side of the frontal ganglion there arises a small nerve, undescribed by former workers. It extends latero-ventrad, to the lower portions of the pharynx. The term *pharyngeal* may be applied to this nerve.

THE RECURRENT NERVE\* (Figs. 4, 7, *r*). The recurrent nerve consists of a single median nerve-cord arising from the caudal border of the frontal ganglion. It extends back passing under the supraoesophageal ganglia, and between the aorta and oesophagus, to terminate in the vagus ganglion (*v*).

THE VAGUS GANGLION (Figs. 4, 7, *u*). This is a minute elongated ganglion, not much wider than the diameter of the recurrent nerve. It is situated 3-4 millimeters caudad of the supraoesophageal ganglion, between the aorta and the oesophagus, and constitutes the termination of the recurrent nerve.

THE STOMOGASTRIC NERVES (Figs. 4 and 7, *st*.) consist of two parallel cords, arising from the caudal border of the vagus ganglion. At the point of emergence from underneath the aorta, they diverge, passing over to either side of the oesophagus, whence they continue caudad, innervating the alimentary canal and terminating in the neighborhood of the mid-intestine.

THE LATERAL OR PAIRED SYMPATHETIC SYSTEM (Figs. 4 and 7). This system is characterized by a pair of small ganglia (*lg*), situated one on either side of the oesophagus and slightly caudad of the pharyngeal constriction. The nerves are quite minute and are confined to the dorsal and lateral portions of the anterior region of the oesophagus.

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\* According to Berlese '07, p. 597, the recurrent nerve is typically double and appears as a single nerve through coalescence.

There seems to be no connection between the two lateral ganglia, nor are these connected with the vagus system as is generally the rule in insects. They are united to the central nervous system by the nerves *u* and *m*. Nerves *u* are attached to the ventral borders of the two halves of the brain and run caudad one on either side of the recurrent nerve until emerging from underneath the aorta to which they are closely joined. At this point, the nerve *u* increases in thickness (*z*) and curving gradually latero-ventrad, finally enters the cephalic portions of the ganglion. Nerve *m* is attached to the ventro-lateral border of the brain and extends caudad along the dorso-lateral portion of the oesophagus. Near its attachment to the brain, it gives off a lateral branch (*x*), which appears like a separate nerve of the brain. Caudad, nerve *m* gives off three branches, the first two of which join the enlarged transverse portion of nerve *u* (labeled *z*). The third branch joins nerve *p* of the same system. Nerve *p*, extending cephalad as a continuation of nerve *z*, innervates the lateral parts of the pharynx, caudad of the crura cerebri. Nerve *q* arises from the anterior lateral part of the ganglion (*lg*) and extends cephalad, passing between the mandibular muscles and the oesophagus, and underneath the optic, antennal and mandibular nerves to the lateral portions of the mouth. Nerve *s* projects caudad from the lateral ganglion, passing for some distance parallel to the stomogastric nerves. It gives off numerous small branches to the sides of the oesophagus.

THE VENTRAL SYMPATHETIC OR SUPERADDED SYSTEM (Figs. 1, 2, 3, 5, and 10).

The ventral sympathetic system consists of a minute MEDIAN NERVE (*mn*.) extending caudad from each of the first eleven ventral ganglia. As a rule, the median nerve gives rise to a pair of lateral branches, the TRANSVERSE OR RESPIRATORY NERVES (*tv. n.*) which extend laterad over of the connectives and nerves of the central system.

The median nerve arising from the suboesophageal ganglion is comparatively short. In a few instances it has been found wanting altogether, so that the transverse nerves arise directly from the ganglion. These transverse nerves are united with the first pair of nerves of the connectives (*n<sub>1</sub>c*).

In the thorax, the median nerves are short and give rise to relatively very large transverse nerves. These extend caudo-laterad over the ventral muscles and unite with the tracheal

nerves (Fig. 2, *tr. n.*) Each transverse nerve of the third thoracic ganglion gives off a small mesal branch, which innervates the small transverse muscles of this region. Before reaching the tracheal nerve, the last mentioned transverse nerve receives branch 5 of the lateral nerve trunk of the first abdominal ganglion.

As a rule, the median nerve of each abdominal segment extends caudad to the anterior border of the following ganglion (Fig. 3). Here it terminates in an enlargement, which may be the GANGLION OF THE MEDIAN NERVE\* (*mg*).

The transverse nerves are two in number for each median nerve. Each extends laterad receiving branch 1 of the lateral nerve and forming with it a single nerve, which connects with the tracheal nerve.

Exceptions to the above typical condition occur in the first and seventh abdominal segments. The median nerve of the former does not give rise to any transverse nerves (Fig. 1) and in the latter the median nerve does not reach the following ganglion but terminates in the two transverse nerves (Fig. 10).

As stated in connection with the mandibular nerve, a minute ganglion is to be found at the base of the mandible, (Fig. 6), forming a part of the sympathetic system. The main nerve 4 enters the mandible and gives off four branches. The caudal termination of nerve 4 has not been traced. Nerves 6 and 7 are also part of this system. Branch 2 connects the ganglion with the central system.

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## EXPLANATION OF PLATES.

FIG. 1. Dorsal aspect of the larva, showing the entire nervous system. The ventral longitudinal muscles have been represented on the right side to illustrate their relation to the nerves.

*1A, 2A, 3A, etc.*, abdominal segments.

*1T, 2T, 3T*, first, second and third thoracic segments.

*I, II, III*, first, second and third thoracic ganglia.

*1-8*, first to eight abdominal ganglia.

*alm*, alimentary canal.

*ant*, antenna.

*d, d, d*, outline of the ventral diaphragm.

*ej. d.*, ejaculatory duct.

*g, g*, tracheal gills.

*in. n.*, intestinal nerve.

*lf, lf*, lateral filaments of the abdominal segments.

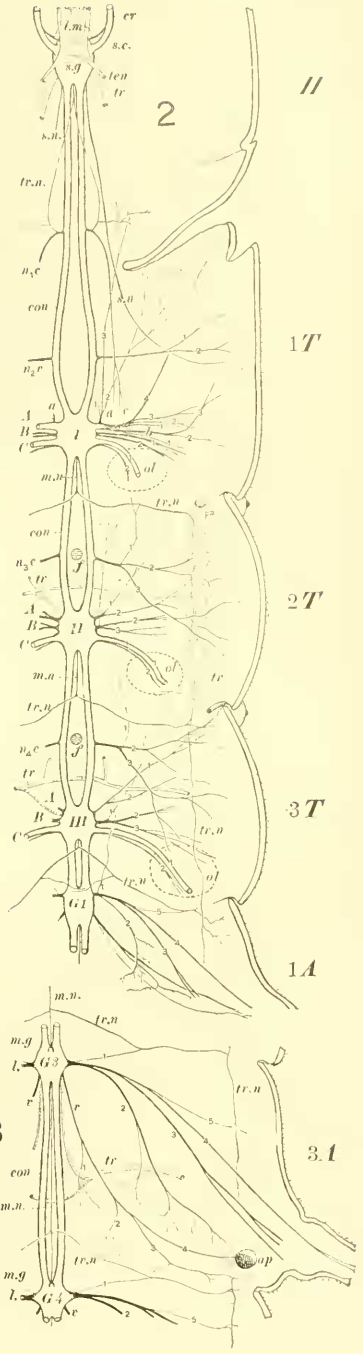
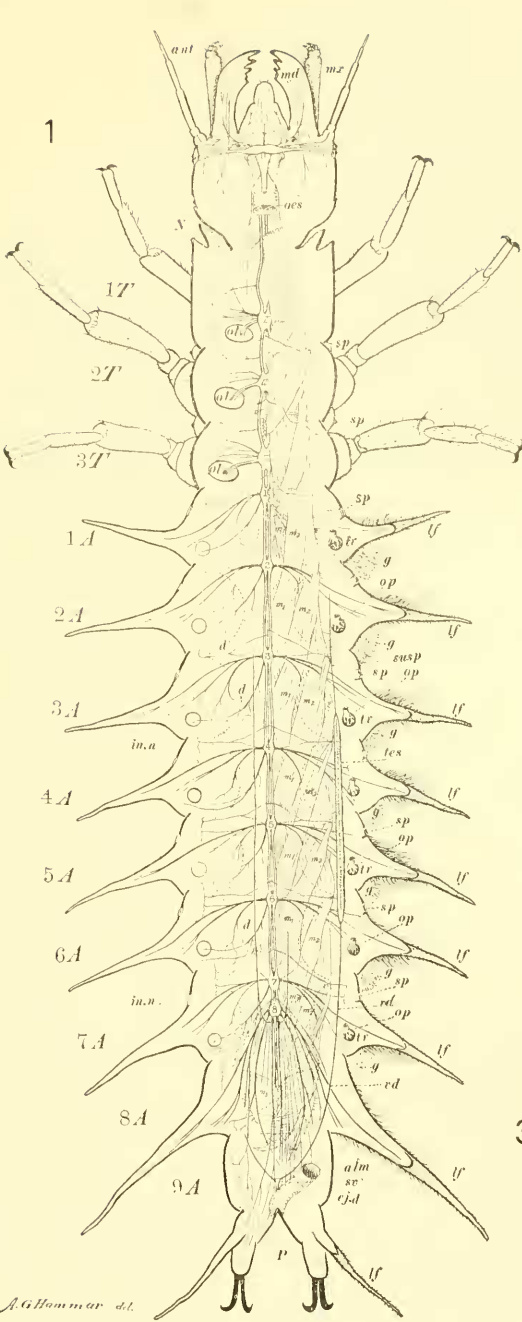
*m<sub>1</sub>, m<sub>2</sub>*, upper-great-ventral-recti-muscles.

*m<sub>3</sub>*, large bundle of muscles in the ninth abdominal segment.

*md*, mandible.

*mx*, maxilla.

*N*, neck.



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*oes.* oesophagus.  
*ol.* opening to the leg.  
*om.* oblique muscles of the first abdominal segment.  
*op.* opening to the tracheal gills.  
*P.* prolegs.  
*sp.* spiracle.  
*susp.* suspensory ligament of the testis.  
*s. v.* seminal vesicle.  
*tes.* testes.  
*tr.* tracheae supplying the gills.  
*vd.* vas deferens.

FIG. 2. Dorsal view of the five anterior ventral ganglia. Lettering as in Figs. 1 and 3.

FIG. 3. Third abdominal segment.

*1A, 3A.* first and third abdominal segments.  
*1T, 2T, 3T.* first, second and third thoracic segments.  
*I, II, III.* first, second and third thoracic ganglia.  
*A, B, L.* nerve trunks of the thoracic ganglia.  
*a, b, c.* branches of nerve *A* of ganglia *I*. *1, 2, 3, 4\**, are sub-branches to same nerve.  
*con.* connective.  
*c. r.* crura cerebri.  
*f.* furcae.  
*G1, G3, G4.* first, third and fourth abdominal ganglia.  
*H.* head.  
*l.* lateral nerve-trunk of abdominal ganglia.  
*lm.* labial muscles.  
*m. g.* minute ganglion of the median nerve.  
*m. n.* median nerve.  
*n<sub>1</sub>c, n<sub>2</sub>c, n<sub>3</sub>c, n<sub>4</sub>c.* first to fourth nerve of the connectives.  
*ol.* opening to the leg.  
*op.* opening to the tracheal gills.  
*s. c.* suboesophageal commissure.  
*s, g.* suboesophageal ganglion.  
*sn.* salivary nerve.  
*ten.* tendon of the labial muscles.  
*tr.* tracheae.  
*tr. n.* tracheal nerve.  
*tv. n.* transverse nerve.  
*v.* ventral nerve-trunk of abdominal ganglia.

FIG. 4. Dorsal view of the head. Lettering as in Fig. 7.

FIG. 5. Ventral view of the head.

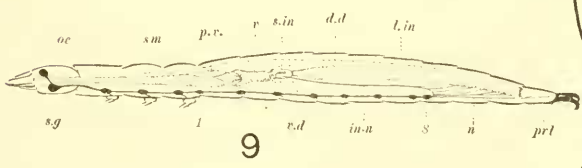
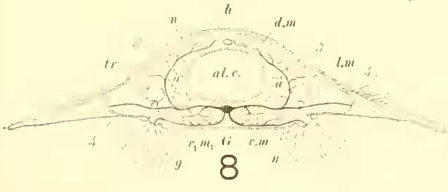
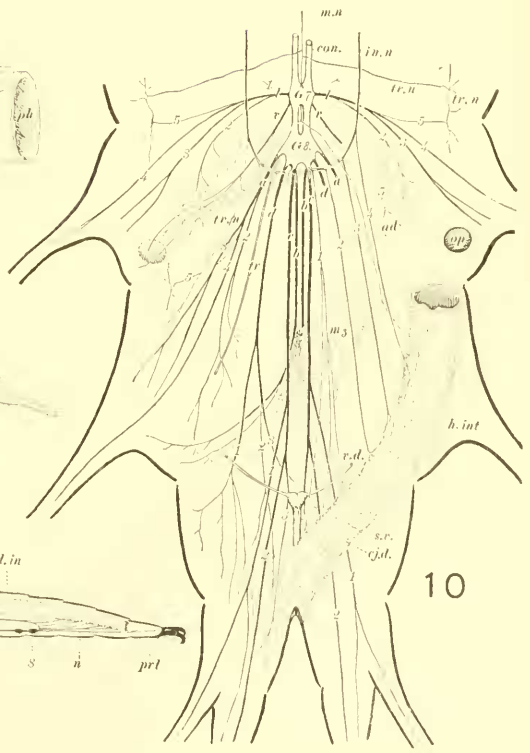
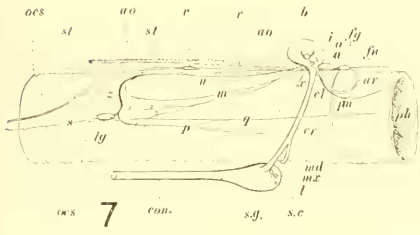
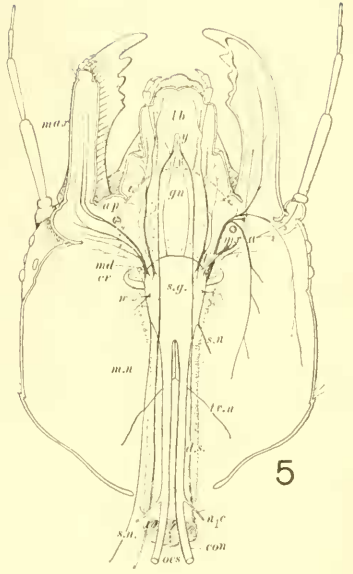
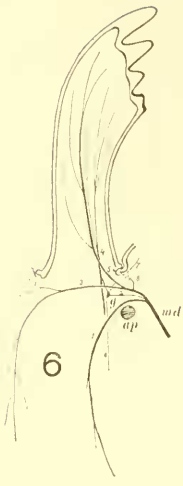
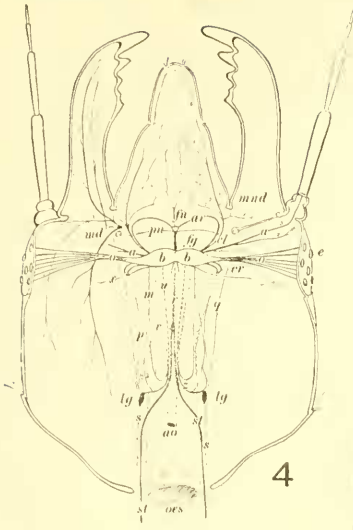
FIG. 6. The mandibular nerve.

FIG. 7. Lateral view of the nerves of the head.

*a.* antennal nerve.  
*ao.* aorta.  
*ap.* apodeme.  
*ar.* arched nerve.  
*b, b.* brain or supraoesophageal ganglia.  
*cl.* clypeo-labral nerve.  
*con.* connective.  
*cr.* crura cerebri.  
*d. s.* salivary duct.  
*e, e.* simple eyes.

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\* Other numbers in these and following figures designate main branches of the different nerve trunks.



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*fg.* frontal ganglion.  
*fn.* frontal nerve.  
*g.* ganglion of the mandibular nerves.  
*gn.* gustatory nerve.  
*i.* nerve connecting the frontal ganglion with the brain.  
*l.* labial nerve.  
*lb.* labium.  
*lg.* lateral ganglion.  
*max.* maxilla.  
*md.* mandibular nerve.  
*m. n.* median nerve.  
*mml.* mandible.  
*m, p, q, s, u, z.* nerves of the lateral sympathetic system.  
*mx.* maxillary nerve.  
*n<sub>1c</sub>.* first nerve of the connective.  
*o.* optic nerve.  
*ocs.* oesophagus.  
*ph.* pharynx.  
*pn.* pharyngeal nerve.  
*r.* recurrent nerve.  
*s. c.* suboesophageal commissure.  
*s. g.* suboesophageal ganglion.  
*s. n.* salivary nerve.  
*st.* stomogastric nerve.  
*t.* trachea in the labium.  
*tn. n.* transverse nerve.  
*v.* vagus ganglion.  
*w.* nerve of the suboesophageal ganglion.  
*x.* nerve of the brain.  
*y.* opening of the salivary ducts.

FIG. 8. Section through an abdominal segment, showing the distribution of the nerves.

*3, 4.* branches of the lateral nerve.  
*a.* adipose tissue.  
*alc.* alimentary canal.  
*d. m.* dorsal muscles.  
*G.* abdominal ganglion.  
*g.* gills.  
*h.* heart.  
*l. m.* lateral muscles.  
*n. n.* nerves.  
*tr.* trachea.  
*v. m.* ventral muscles.  
*v<sub>1m<sub>1</sub></sub>*, fibers of the ventral muscles passing over the nerves (compare with Fig. 1, *m<sub>2</sub>*).

FIG. 9. Lateral view of the larva showing the attachment of the intestinal nerve. (Compare with Figs. 1 and 10).

*1-8.* first to eighth abdominal ganglia.  
*d. d.* dorsal diaphragm.  
*in. n.* intestinal nerve.  
*l. in.* large intestine.  
*n.* nerve of the terminal ganglion.  
*oc.* oesophagus.  
*prl.* proleg.  
*p. v.* proventriculus.  
*s. g.* suboesophageal ganglion.  
*s. in.* small intestine.  
*sm.* suspensory muscles of the alimentary canal.  
*v.* ventricle.  
*v. d.* ventral diaphragm.

- FIG. 10. Terminal portion of the nervous system of the abdomen.  
*a, b, c, d.* nerve-trunks of the terminal ganglion.  
*ad.* adipose tissue.  
*con.* connective.  
*ej. d.* ejaculatory duct.  
*G7, G8.* seventh and eighth abdominal ganglia.  
*h. int.* hind intestine.  
*in. n.* intestinal nerve.  
*l.* lateral nerve-trunk.  
*m. n.* median nerve.  
*m<sub>s</sub>.* bundle of muscles in the eighth abdominal segment.  
*op.* opening to the tracheal gills.  
*s. v.* seminal vesicle.  
*tr.* trachea.  
*tr. n.* tracheal nerve.  
*tv. n.* transverse nerve.  
*v.* ventral nerve-trunk.  
*v. d.* vas deferens.

## A CASE OF GREGARIOUS SLEEPING HABITS AMONG ACULEATE HYMENOPTERA.

By J. CHESTER BRADLEY.

Mr. Banks\* has summarized what was recorded up to the time he wrote concerning the sleeping habits of Hymenoptera. Briefly, this consisted of several observations of usually solitary aculeates either sleeping in flowers or clinging to twigs. Belfrage has observed *Scolia lecontei* "during the night and chilly weather in clusters, closely attached to the stems of grass and plants."

Mr. Banks' observations were made in a small patch of timothy, orchard grass and wild onion. Here he found specimens of three species of *Ammophila*, of two bees, and of *Myzine sexcincta* sleeping, but always only *one* individual on the same stem of grass. Night after night they would appear between seven and eight, and leave before five the next morning. Gradually they became less numerous. Near the patch was a field of recently cut rye, where he surmises they may previously have rested, and also a garden and bean patch.

Mr. Schwarz† records observing in southwestern Texas within a short space, four dead shrubs of *Celtis pallida* which harbored from fifty to seventy specimens of two species of bees asleep, and near at hand other shrubs with a smaller number of specimens.

\* Journ. N. Y. Ent. Soc. Vol. X, p. 209.

† Proc. Entom. Soc. Wash., IV, p. 24.